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Process studies of dissolved organic carbon and bacterioplankton in the ocean

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Summary

The oceans play an important role in the global climate system by mediating as buffer of heat and greenhouse gasses (e.g. CO₂). Oceanic water constitutes one of the largest carbon (C) reservoirs of the earth and the fluxes of carbon in the marine system affect the global biogeochemical cycle of carbon. Oceanic uptake of atmospheric CO₂ results mainly from photosynthesis by phytoplankton (primary production). A portion of this newly fixed organic matter is eventually transformed into a dissolved phase. The export of particulate and dissolved organic carbon, from the surface layers to deep water and eventually burial of carbon on the sea floor, results in a net reduction of the atmospheric CO₂ concentration. To quantify and understand the physical and biological controls on these fluxes is the primary objective of the Joint Global Ocean Flux Study (JGOFS). The research encompassed in this thesis was carried out within the JGOFS framework or related projects.

The upper ocean is the principal site of organic matter production and recycling. Carbon fixed by the phytoplankton community is partly released into the dissolved phase in seawater. Heterotrophic bacteria mediate in the transformation of this dissolved organic carbon (DOC), throughout the water column. Quantitative studies show that the major fluxes of carbon in the euphotic zone occur in this 'microbial loop' and bacteria dominating carbon biomass in oligotrophic oceans. Apart from the unknown underlying mechanisms, microbial processes are therefore a major flux in the global carbon cycling and bacteria are a significant component of the marine ecosystem.

Oceanic DOC represents one of the largest pools (~740 GtC) of reduced carbon on earth, yet little is known about the characterisation, transformation or absolute concentration of DOC in seawater. Until recently, DOC was not considered to be important to the global biogeochemical cycle of carbon. Renewed interest in DOC was initiated by the introduction of a new high temperature combustion (HTC) method, initially yielding 2-3 times higher values than those previously observed. Recent re-evaluations and improvement of the HTC method, with special emphasis on the blank correction and instrument performance, have facilitated reliable quantification of marine DOC. But quality control of DOC analysis remains decisive (see chapter 2). High values of the HTC-method, published over the last decade, proved to be overestimates due to high system blanks and improper data analysis.

A study in the Southern Ocean (chapter 3) along 62°E (France-JGOFS / ANTARES 2) has demonstrated mixed layer concentrations of organic carbon between 52 μM C in the Antarctic Divergence (64°S) and 63 μM C in the Polar Frontal Zone (49°S). Vertical profiles showed a slight, but significant, decrease in organic carbon below the mixed layer, to about 42 μM C below 2000 m across the transect. The homogeneity and low concentration of organic carbon in deep water is consistent with recently analyzed samples from the Atlantic Ocean (DCM-1996) and NW Indian Ocean (US GLOBEC2). The study in the (sub)tropical Atlantic Ocean (Chapter 2) has demonstrated no significant difference between the concentration of DOC in the main deep watermasses (Antarctic Intermediate Water, North Atlantic Deep Water and Antarctic Bottom Water), despite the marked difference in oxygen and nutrient concentration. The comparison of vertical profiles of

DOC in different ocean basins (chapter 2) supports the evidence for a constant deep water DOC concentration, comprised of biologically resistant material. Besides, the homogeneous low value ($\sim 40 \mu\text{M C}$) below ca. 1000 m depth provides a first approximation to validate comparisons between different data sets.

Although the most recent DOC data show values generally similar to those reported in past decades (e.g. Duursma, 1961), the improved accuracy and precision of modern analyses allow the detection of significant differences in the DOC pool in the ocean, which is important to microbiological and elemental flux studies. Whereas it was observed that DOC was homogeneously distributed in the deep ocean, significant difference in the surface layer and at intermediate depth were apparent. Despite the relatively low concentration of DOC in the mixed layer of the Southern Ocean, organic carbon showed a trend with corresponding measurements of phytoplankton biomass and bacterial production (Chapter 3), underlining the dependence of bacterial growth on a pool of 'freshly' produced DOC. A study in the northern North Sea (Chapter 4) has demonstrated enhanced DOC concentration ($86.1 \pm 4.8 \mu\text{M C}$) during a phytoplankton bloom, relative to pre-bloom conditions ($73.3 \pm 0.5 \mu\text{M C}$). The relative increase in the carbon stock (0.6 mol C m^{-2}) of DOC in the photic zone contributed significantly to the overall atmospheric carbon sink of the bloom. In contrast, the distribution of DOC in the estuary of the western Wadden Sea (Chapter 4) was mainly driven by physical processes of the system (e.g. mixing). Besides, mixing simulations carried out in the laboratory, indicate additional non-conservative behaviour of DOC during estuarine mixing. Although global non-conservative behaviour has been confirmed for several metals (e.g. Fe and Mn) and humic acids, this has not been reported for DOC. In contrast to previous studies, these results indicate the importance of DOC dynamics in coastal carbon cycling and flocculation processes as mechanism for the control of riverine input of organic matter to the ocean.

Organic carbon, in the depth range between the mixed layer and the oxygen minimum, was found (chapters 2 and 3) to exhibit a modest inverse trend versus apparent oxygen utilisation (AOU). The stoichiometry of this trend suggests that only a minor fraction of the oxygen consumption in the open ocean would be due to remineralization of DOC, though the underlying processes remain to be resolved. With the potential to serve as an active intermediate in the remineralisation of organic matter, the transfer of carbon through the DOC pool has an important control on the flux of carbon in the ocean. Presumably, this involves only a minor ($<10\%$) fraction of the DOC pool, by far the largest fraction remains refractive (i.e. biological insignificant).

Ultimately, the supply of labile DOC is a key factor controlling the productivity of bacterioplankton. Heterotrophic bacterioplankton mediates in particle-dissolved transition and the remineralisation of organic matter, thereby in their turn effecting the distribution of DOC, oxygen and nutrients in the water column. The natural variability in bacterial production is poorly understood. In this thesis it is described how bacterioplankton responds to variable environmental conditions on different spatial and temporal scales. Chapter 5 describes the abundance and productivity of bacterioplankton in relation to seasonal upwelling in the NW Indian Ocean. The diversity in relative importance of physical and biological processes was reflected in a broad range of both phyto- and bacterioplankton production. Heterotrophic activity and primary production were closely correlated, indicating the dependence of bacterioplankton on local phytoplankton-derived organic carbon and their ability to adapt quickly to changes in the environment.

Apparently, the highest bacterial production occurs during enrichment of the surface water in the Somali current, related to upwelling of cold, nutrient-rich, deep water during the SW-monsoon. In contrast, the Gulf of Aden and the Red Sea were shown to be most productive during the NE-monsoon. In the NW Indian Ocean bacterial production, controlled by the supply of labile DOC, was vertically uncoupled from primary production and extended below the euphotic zone (0-35 m) to the mixing depth of ca. 100 m. Apparently, the climatological conditions prevailing during the SW-monsoon result in a (temporal) uncoupling of organic matter production, export and decomposition.

Chapter 6 and 7 describe a contrasting scenario in the (sub)tropical north Atlantic Ocean where there is evidence of a strong co-variance of bacterial production rates and vertical distribution of autotrophic carbon assimilation in a stratified system as opposed to the NW Indian Ocean. When converted to heterotrophic carbon production with traditional conversion factors the summer population in the (sub)tropical north Atlantic Ocean showed an overall relatively low integrated bacterial carbon production equivalent to <9% of primary production. Little variability in the ratio of bacterial production to primary production (BB:PP) between different sites, suggests strong coupling between the two groups. This uniform coupling of daily rates of heterotrophic versus autotrophic production in the oligotrophic ocean is in keeping with the notion that in situ recycling of nutrients by the heterotrophic food web continuously supports primary production. In the NW Indian Ocean driven by seasonality of monsoons the BP:PP ratio appeared to be consistently higher (0.09-0.34), supporting the hypothesis that the ratio is generally low under quasi-steady state conditions in oceanic waters as encountered in the (sub)tropical Atlantic.

The apparent coupling between measured rates of DNA and protein synthesis, using tritium-labelled tracer incorporation assays (chapters 5 and 6), suggests maintenance of balanced bacterial growth, underlain by significant diel variations in cell abundance and growth parameters of the bacterioplankton. Diel patterns are not uncommon in prokaryotic organisms, i.e. phototrophic prokaryotes (cyanobacteria) are well known to exhibit circadian expression of several growth properties and the effect of light on the in situ cell cycle has been shown to cause synchronised cell division of the widespread oceanic prokaryotes *Synechococcus* spp. and *Prochlorococcus* spp. In contrast, daily patterns and in situ variability of heterotrophic bacteria in the oceans are far less documented. Chapter 7 reports the first coherent set of field observations of diel cycles of biomass and production of heterotrophic bacteria. Maximum synthesis of DNA after midnight into dawn is followed by an increase in cell numbers in daytime, due to cell division. The diurnal variability of bacterial abundance, with a minimum near sunrise and a maximum near sunset, accounted for ~30% variation of station mean integrated bacterial abundance (0-200 m). The diel oscillation of protein synthesis is synchronous with DNA synthesis but with relatively lower amplitude. The simultaneous observations of the DNA doubling and division cycle of the phototrophic prokaryotes show a trend distinctly opposite of the DNA cell cycle of the heterotrophic bacteria. Minor day-to-day variability of in situ primary production and coupling of heterotrophic versus autotrophic production warrants our expectation of diel cycles of heterotrophs, consistent with known circadian oscillations of phototrophic prokaryotes, observed simultaneously. Until now the tendency in most bacterioplankton studies to reduce variability by averaging

observations (based on short-time incubations) over the sample period, have largely obscured any conceivable diel changes.

The diel periodicity of heterotrophic bacteria reported in chapter 7 might be truly intrinsic (bioclock) but could also be affected by periodicity of substrate abundance of labile organic matter associated with phytoplankton dynamics. The circadian rhythm of phytoplankton almost inevitably yields a diel periodicity of supply and abundance of dissolved organic matter. The exact diel maxima and minima of substrates currently are not known, but diel changes of the DOC pool would hardly be discernible at the current reproducibility of $\sim 1 \mu\text{M C}$ (Chapter 2).

Specifically designed incubation experiments (chapter 8) indicate that bacterial growth rates typically exceed 0.6 d^{-1} , which is close to the in situ specific growth rates (μ_{cell}) estimated as the observed difference in bacterial abundance's between dawn and dusk (chapter 7). Alternatively, an independent estimates of the bacterial growth rate was obtained by the physiological approach (chapters 5, 6, 7 and 8), focusing on the incorporation of labelled precursors, i.e. radiotracers. The ^3H -thymidine incorporation rates yield in situ growth rates (μ_{DNA}) of $\sim 0.03 \text{ d}^{-1}$, remarkably lower compared to μ_{cell} , but within the range reported in recent studies which use radiotracer incorporation techniques. Given the high growth rate of phototrophic prokaryotes (~ 1 doubling per day), the μ_{DNA} , in the order of days to weeks, is remarkably low. Traditionally, bacterial production is estimated using assumed mean oceanic values of the conversion factor (CF) empirically derived from incubation experiments (chapter 8). This concept appears to be questionable, since the dynamics of the natural occurring heterotrophic assemblages complicate the use of such incubations to estimate CF. In Chapter 8 the CF is re-evaluated, taking into account the proportion dividing cells based on cell specific DNA content quantified by flow cytometry. Application of the new CF yields μ_{DNA} for the heterotrophs of $\sim 0.3 \text{ d}^{-1}$, essentially similar to the computed heterotrophic μ_{cell} and the growth rate of the phototrophic prokaryotes, providing robust evidence for high in situ growth rates of heterotrophic bacterioplankton in the ocean. In other words the traditionally applied CF values were apparently suffering from a large portion of non-viable, non-dividing cells, thus underestimating the division rate of the small portion of viable, dividing cells. The now proven high growth rates of heterotrophic bacteria are in agreement with the hypotheses of strong coupling between autotrophic and heterotrophic processes in the oligotrophic ocean, ultimate at the diel level. The diel cycles reported in this thesis have important implications for the quantitative analysis of microbial processes in the marine system. Besides, they provide evidence that bacterial production and derived growth rates of heterotrophic bacteria might in the past have been underestimated by one order of magnitude due to the use of traditional CF values.